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Prey vulnerability and predation pressure shape predator-induced changes in O_2 consumption and antipredator behaviour

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Predators regulate prey abundance (direct predation) as well as influencing their metabolism and behaviour (indirect effects) through the perception of risk. Antipredator traits are informed by individual experience of risk, which may vary over environmental gradients and through ontogeny. As prey grow, individual vulnerability generally diminishes, and the reduction in individual vulnerability with ontogenetic growth can potentially lead to size refugia, ultimately nullifying the impacts of direct predation. Despite the ecological importance of the indirect effects of predation and the disproportionate influence larger individuals have on ecological level processes, there has been little focus on the potential indirect effects of predation risk on invulnerable prey. Using a combination of field and laboratory experiments, we measured the changes in routine oxygen consumption of vulnerable and invulnerable size classes of the intertidal snail *Nucella lapillus* (dogwhelk), exposed to effluent from its crab predator *Carcinus maenas*. To test the potential influence of prior experience of predation risk, measurements were conducted on populations naturally exposed to different levels of predation pressure. Field results showed that only invulnerable snails modified their routine oxygen consumption in the presence of risk, and this occurred across all populations. Oxygen consumption rates in the laboratory, however, contradicted the pattern, with only vulnerable prey responding to the perception of risk. Metabolic responses of both vulnerable and invulnerable prey under field and laboratory conditions are discussed in the context of asset protection and prey energetic state. Observations of snail behaviour in the laboratory showed that dogwhelks from exposed shores, where predatory risk is higher, were more likely to exhibit antipredator behaviour. Importantly, our findings provide evidence that the indirect effects of predators remain influential even after prey are no longer susceptible to direct predation and add to the growing body of evidence highlighting the ecological importance of indirect predation.

Keywords: antipredator behaviour, indirect effects, *Nucella lapillus*, oxygen consumption, physiological response, predation, size refuge, threat-sensitive behaviour, trait-mediated indirect interaction (TMII), vulnerability

In many species, exposure to a predatory cue elicits a series of coordinated, adaptive physiological responses, which influence antipredator behaviour (Hawlena, Kress, Dufresne, & Schmitz, 2011; Van Dievel, Janssens, & Stoks, 2016) and may come at an energetic cost (Hawlena & Schmitz, 2010; Kamenos, Calosi, & Moore, 2006; Slos & Stoks, 2008). Such physiological and behavioural responses, as well as promoting prey survival, lead to localized reductions in foraging rates or changes in habitat use that can cause trophic cascades with lasting effects on local population densities and community structure (Schmitz, Beckerman, & O'Brien, 1997; Schmitz, Krivan, & Ovadia, 2004; Trussell, Ewanchuk, Bertness, & Silliman, 2004; Werner & Peacor, 2003). The energetic costs of predator-induced stress responses have been suggested as potential explanations for reductions in prey fitness, and consequently changes in prey demography (Boonstra, Hik, Singleton, & Tinnikov, 1998; Creel, Christianson, Liley, & Winnie, 2007; Preisser, Orrock, & Schmitz, 2007; Slos & Stoks, 2008), ecosystem nutrient dynamics (Hawlena & Schmitz, 2010), energy flow through trophic levels (C M Matassa & Trussell, 2014) and may possibly account for food chain length in some systems (Trussell, Ewanchuk, & Matassa, 2006b).

The threat of predation varies both temporally and spatially at the individual and population level (Lima & Bednekoff, 1999; Lima & Dill, 1990). Natural variation in ambient predation pressure among populations has led to the evolution of adaptive physiological and behavioural responses to predation, which may be adjusted by local conditions (Donelan & Trussell, 2018; Handelsman et al., 2013; Holopainen, Aho, Vornanen, & Huuskonen, 1997). For example, the resting metabolic rate of frog tadpoles, *Rana temporaria*, exposed to short-term risk increases,

leading to an enhanced ability to escape predators. However, with longer exposure metabolic rates drop, showing acclimation to predator risk by reducing energetic demands which may underpin risk-averse behaviour while foraging (Steiner & Van Buskirk, 2009). This individual experience of local predation pressure can also inform the subsequent generation, through epigenetic programming (Jablonka & Raz, 2009; Love, Mcgowan, & Sheriff, 2013). This trait is particularly important for direct developing offspring, whose experience of risk is likely to correlate strongly with that of their parents (Dixon & Agarwala, 1999; Poethke, Weisser, & Hovestadt, 2010). For instance, offspring dispersal (a predator avoidance trait) in the lizard *Zootoca vivipara* increases as a consequence of maternal predator-related stress, decreasing the potential predation pressure experienced by offspring during the most vulnerable stages of development (Bestion, Teyssier, Aubret, Clobert, & Cote, 2014). In this way, parental input and individual experience combine to produce more suitable adaptive ecotypes (Donelan & Trussell, 2015; Giesing, Suski, Warner, & Bell, 2011) with natural selection acting to reinforce local adaptations (Guerra-Varela et al., 2009; Mäkinen et al., 2008).

At the level of the individual, several factors including learned behaviours and ontogenetic somatic growth can result in a change in the suite of predators that threaten prey and, in many cases, result in a reduction in overall predation pressure (Paradis, Pepin, & Brown, 1996; Scharf, Juanes, & Rountree, 2000). Larvae of the three-spined stickleback, *Gasterosteus aculeatus*, use predator size relative to their own as a measure of predation risk and modify their foraging behaviour accordingly, thus optimizing energy intake while minimizing the risk of being eaten (Bishop & Brown, 1992). This type of threat-sensitive behaviour is further enhanced when prey are able to adjust their behaviour relative to their encounter rates with different predators (Rochette, Maltais, Dill, & Himmelman, 1999). Legault and Himmelman (1993) showed that this kind of threat-sensitive behaviour exists in several marine invertebrate

prey, but that correlations between encounter rates and antipredator behaviour vary between species.

Ontogenetic somatic growth can be an escape strategy in and of itself, with many prey species able to grow to size refugia and escape direct predation completely (Chase, 1999). Little is known regarding the way in which prey that have reached a size refuge respond to the threat of predation (Lundvall, Svanbäck, Persson, & Byström, 1999; Werner et al., 1983), although links between size-related vulnerability and antipredator behaviour have been shown in certain aquatic gastropods (DeWitt, Sih, & Hucko, 1999; Rochette & Himmelman, 1996). In their study into the potential for the aquatic snail *Physa gyrina* to express behavioural compensation for morphological vulnerability to a crayfish predator (*Orconectes rusticus*), DeWitt et al (1999) showed that larger less vulnerable snails demonstrate reduced levels of antipredator behaviour. Considering the disproportionate impact larger individuals have on demography and resources (Etter, 1989; Paine, 1976), it is perhaps surprising that little interest has been shown in the indirect effects predators have on prey that have reached size refugia.

The purpose of this study was to investigate how differences in prey size, and hence vulnerability to direct predation, affect the physiological and antipredator response in prey. In addition, we examined how these effects were modified by prior experience of predation risk, based on habitat (sheltered or exposed shores). We used a widely adopted intertidal predator–prey system and implemented a series of field and laboratory experiments, to examine both physiological and behavioural responses of vulnerable and invulnerable prey to predation risk.

<H1>Methods

<H2>Predator–prey system

The green shore crab, *Carcinus maenas*, is an important predator of the dogwhelk, *Nucella lapillus* (hereafter referred to as *Nucella*). Both species are found extensively across the North

Atlantic and co-occur along a gradient of wave exposure (Crothers 1985). *Nucella* reaches a size refuge from crab predation at 27 mm shell length (Hughes & Elner, 1979). As with many gastropod species, *Nucella* are able to assess predation risk through the detection of differences in concentration of kairomones, waterborne chemical cues inadvertently released by predators (Edgell, 2010; Catherine M. Matassa & Trussell, 2011; Vadas, Burrows, & Hughes, 1994). *Nucella* use differences in the concentration of these chemicals to assess the proximity of a predator (Freeman & Hamer, 2009; Large, Smee, & Trussell, 2011) and therefore are influenced by local hydrodynamic conditions (Freeman & Hamer, 2009; Large et al., 2011). For example, in high-flow, wave-exposed environments, characterized by an elevated degree of mixing, the homogenization of the olfactory seascape created by predatory kairomones affects the chemoreceptive ability of prey (Large et al., 2011; Weissburg, James, Smee, & Webster, 2003; Zimmer & Butman, 2000). Large et al (2011) showed that antipredator behaviour in *N. lapillus* is strongly influenced by hydrodynamic mixing and that *Nucella* chemoreception ability is reduced in very slow- or fast-flowing turbulent water. They argued that on exposed shores, due to the homogenization of different concentrations of chemical cues, *Nucella* are unable to perceive predation risk. Wave action also directly impacts the densities of crabs, with wave exposure being negatively correlated with crab densities (Hughes & Elner, 1979; Large & Smee, 2013; Menge, 1983; Rochette, Smee, & Trussell, 2011). Hence populations of *Nucella* can experience varying levels of predation risk depending on local wave action regimes (Freeman & Hamer, 2009; Large et al., 2011; Menge, 1976; Tyler, Stafford, & Leighton, 2014). The effects of wave action combined with inherent differences in predator densities result in the formation of distinct ecotypes of *Nucella*, with plasticity present in both morphological and behavioural antipredator traits (Crothers, 1983; Guerra-Varela et al., 2009; Large & Smee, 2013; Rolán, Guerra-Varela, Colson, Hughes, & Rolan-Alvarez, 2004).

139 **<H2>Site selection and predator numbers**

140

141 Our field study was conducted at six sites, three wave-exposed and three wave-sheltered,
142 around the coasts of Anglesey, North Wales, U.K. (Fig. 1). Sites were initially selected as
143 wave-sheltered or wave-exposed based on community structure (Ballantine, 1961) and later
144 exposure was calculated using the map-based method to estimate mean wave fetch for each
145 site (Burrows, Harvey, & Robb, 2008). To estimate differences in crab abundance, baited crab
146 traps (60 x 40 cm and 35 cm high, with 500 g of fish) were used at each of the six sites. For
147 each site, crab numbers per trap were counted on 3 consecutive days. A single baited crab trap
148 was placed in the midzone and left for two complete tidal cycles, sampled and then redeployed
149 a further two times, each time ca. 30 m along the shore from the previous location. This allowed
150 us to average crab numbers across the 3 days for each site to provide a mean crab number per
151 trap per site.

152

153 **<H2>Field measurements**

154 We compared field oxygen consumption rates of two size classes of *Nucella* from exposed (low
155 predator abundance) and sheltered (high predator abundance) shores with and without a
156 predator cue. Small *Nucella*, considered vulnerable to predation (N = 7 at each site, mean shell
157 length 14.6 ± SD 1.3 mm) and large, considered invulnerable (N = 7 at each site, mean shell
158 length 29.0 ± SD 1.6 mm) were collected from the same tidal height to control for any unknown
159 shore level size gradients (Elner & Hughes, 1978). Field measurements were conducted
160 between 1100 and 1700 on 4–8 October 2017, apart from one sheltered shore which had to be
161 completed during the next tidal cycle (17 October 2017) due to adverse weather conditions.
162 Animals were collected before being exposed to air, as the tide was receding, and subsequently
163 were kept submerged to avoid any potential impacts on oxygen consumption rates (McMahon,

1988; Stickle, Moore, & Bayne, 1985). Care was taken not to select individuals that were actively feeding. Individual *Nucella* were carefully placed into closed system respirometers (70 x 70 mm and 50 mm high) containing fully aerated filtered sea water to determine oxygen consumption rates. All water used in field measurements was sourced from the laboratories at the School of Ocean Sciences, Bangor University, Menai Bridge, U.K. Changes in water oxygen partial pressure (PO_2) were measured using an optical fluorescence technique (PreSens, Regensburg, Germany, Fibox 4 trace, Fiber Optic Trace Oxygen Meter). Each respirometer was equipped with a single oxygen sensor spot (PreSens) located on the inside of the lid, which allowed for nonintrusive measurement of sea water PO_2 levels at regular intervals. The seawater was filtered (0.45 μm) to reduce contaminating effects of biological activity from microbes and algae, and two controls consisting of respirometers without snails were included during each trial (N=16). Controls for filtered sea water and crab effluent were used to assess any background (microbial) oxygen consumption rates and this was then subtracted from all other measurements in that trial. Sea surface temperature was measured at each site at the beginning of each experiment and respirometers were placed into temperature-controlled water baths to ensure that in situ temperatures were maintained throughout the period of oxygen consumption measurement (mean 14.18 ± SD 0.06 ^{o}C across all sites) to prevent temperature-related changes in metabolic rates (Dahlhoff, Stillman, & Menge, 2008).

Preliminary trials showed that rates of oxygen consumption were initially elevated when *Nucella* were first placed in the respirometers due to handling stress, but levels fell over the next 25 min as snails settled in the respirometers. Over the next 45 min PO_2 levels fell within the respirometers in a linear fashion which we considered to be routine rates of oxygen consumption as the snails were free to move around within the respirometers. Several studies have shown that exposure to crab effluent influences *Nucella* behaviour and therefore the use of routine rates of oxygen uptake are more appropriate when determining the natural reaction

of *Nucella* to the detection of a predator (including the effects of movement). Based on these initial observations, individual snails were inserted into their respiration chambers, sealed and left for 25 min before the initial PO_2 reading was taken. Repeated PO_2 readings were then taken every 5 min for the next 45 min to determine the linear fall in PO_2 over time. Snails therefore spent 70 min in total in their respective respirometers. In each case, care was taken to avoid hypoxia from developing within the respirometers by ensuring that PO_2 levels remained above 17 kPa throughout this period. Rates of oxygen consumption were determined from the drop in PO_2 over 45 min by linear regression, minus the background fall in PO_2 from the respective controls. This value was multiplied by the solubility coefficient for oxygen adjusted for salinity and temperature to give whole-body values in ml O_2/h. Values were corrected to STPD (standard temperature and pressure and dry) and expressed as μmol O_2/h.

Once a baseline oxygen consumption rate had been established for each snail, they were then subjected to the predation risk treatment. Each snail that had been monitored for baseline oxygen consumption was exposed to predation risk by exchanging the water in the respirometer for water treated through exposure to crabs. This 'predation risk' water was created in the field by adding 8–10 large male crabs (mean carapace length ± SD 56.6 ± 4.8 mm) to 20 litres of filtered and aerated water for 1 h. *Nucella* were kept submerged during the water change. They were then allowed a further 25 min to acclimatize to the new treatment. Once measurements were complete, all *Nucella* were marked and returned to the laboratory to assess their oxygen consumption rates and behavioural responses to predation risk under controlled laboratory conditions.

<H2>Laboratory measurements

Individuals collected from the field were housed in a temperature-controlled aquarium at similar temperatures to those in the field (mean 13.9 ± SD 0.9 ^{o}C) in fully aerated, recirculated,

natural sea water for 1 month before being used in the second experiment. *Nucella* were not exposed to predation risk during this period. They were fed mussels and barnacles ad libitum and then starved for 48 h before their oxygen consumption was measured, to standardize digestive state (C M Matassa & Trussell, 2014). Laboratory measurements followed the same protocol as the field experiment with routine oxygen consumption rates being established prior to measuring them under predation risk conditions. Water temperature was maintained at the respective in situ temperatures. After 25 min of acclimatization, oxygen consumption rates were measured every 5 min for 45 min. As with the field experiment, the same individuals were then exposed to crab effluent and their oxygen consumption rates were measured.

To determine whether the two size classes of *Nucella* show typical antipredator responses (cessation of movement, Freeman, Dernbach, Marcos, & Koob, 2014; Vadas et al., 1994), they were observed for 20 s every 5 min, over 45 min, and their precise location noted on a diagram of the respirometer following the approach of Large et al. (2011). Care was taken not to cast a shadow over the respiration chambers to reduce any potential impacts on *Nucella* behaviour. As the exact movement of individuals between 5 min increments could not be known, we used the shortest possible distance between two consecutive increments for our calculations. By combining the distance travelled between all increments, we were able to estimate the total distance travelled during the experiment.

<H2>Statistical analysis

As the focus of this study was on comparing the effect of predation risk on oxygen consumption rates of vulnerable and invulnerable prey and not directly on the effects of size, analysis was conducted on whole animal rates of oxygen consumption (Dahlhoff et al., 2008; Hayes, 2001; Packard & Boardman, 1999). To assess the potential impact of predation risk on the oxygen consumption rates of vulnerable and invulnerable prey both in the field and in the laboratory,

we used a model selection approach using gamma distributed generalized linear mixed models (GLMMs). In both analyses, we used whole animal oxygen consumption rates as a response variable and wave exposure (exposed and sheltered), *Nucella* vulnerability (vulnerable and invulnerable) and predation risk treatment (no predator cue and predator cue) as fully crossed fixed effects. Log-transformed total length was used as a covariate to account for any potential size-related differences within the size ranges selected. We considered site as being nested within wave exposure and *Nucella* ID as a repeated measure (both treated as random effects). We also performed a GLMM with *Nucella* movement as a response variable using the same fixed, nested and repeated terms effects as in previous analyses. The movement results showed overdispersion and were therefore analysed using a negative binomial GLMM. We used the glmm.TMB package to analyse movement results (Brooks et al., 2017).

All GLMMs were constructed and compared in R 3.5.0 (R Core Team, 2013) using the lme4 package (Bates, Mächler, Bolker, & Walker, 2015). Backward model selection was achieved using the drop1 function and models with the lowest Akaike information criterion (AIC) were selected (Bolker et al., 2008). When interaction terms were significant at the $\alpha = 0.05$ level, Tukey post hoc tests were carried out using the emmeans package (Lenth, Singmann, Love, Buerkner, & Herve, 2004).

<H2>Ethical Note.

Our experimental protocol complies with all institutional guidelines at Bangor University. No animals were harmed during the experiment. After the experiment, each whelk was returned to its collection location. No permit was necessary to perform the experiments described above.

<H1>Results

<H2>Field results

Exposure calculations (measured as average wave fetch per site) using the Burrows et al. (2008) map-based method concurred with our assessment of exposure with sheltered and exposed shores having a mean wave fetch of 17.89 km (± 7.77 SD) and 49.55 km (± 10.09 SD), respectively. These values agree with Burrows et al. (2008) assessment of wave-sheltered and wave-exposed shores which they defined as being 20–40 km and 40–60 km, respectively. There was a significant effect of wave exposure on crab numbers per trap (ANOVA: $F_{1,11}$ = 7.42, P = 0.016; Table 1), with wave-exposed sites having an average of 0.89 ± 0.42 crabs per trap compared with wave-sheltered sites which had an average of 41.22 ± 5.81 crabs per trap (Fig. 2). The combination of wave exposure effects on the perception of kairomones (Freeman & Hamer, 2009; Large et al., 2011) and the stark difference in predator densities indicate that *Nucella* were exposed to different levels of predation risk at the two types of site.

The addition of *Nucella* shell length to all models tested had no impact on the AIC calculated and it was therefore not included in further analysis. Model selection results for our field and laboratory measurements are summarized in Table 2. Background respiration rates were 0.52 µmol O_2/h across treatments. Oxygen consumption rates of vulnerable *Nucella* (mean 3.60 µmol O_2/h, SE = 0.25) were lower than those of invulnerable individuals (mean = 16.65 µmol/l/h, SE = 0.85) across all exposure gradients and treatments (gamma distributed GLMM: N = 65, χ^2_1 = 66.12, P < 0.001; Fig. 3). GLMM analysis showed that the two size classes of *Nucella* reacted differently when exposed to crab effluent (gamma distributed GLMM: N = 65, χ^2_1 = 8.85, P = 0.003). Further post hoc analysis showed that in the presence of predation risk, invulnerable *Nucella* reduced their respiration rates by 36.2% (Table A1), whereas

vulnerable individuals showed a slight nonsignificant increase in oxygen consumption rates of 6.01% (Table A1). This pattern was consistent across both exposure levels (gamma distributed GLMM: $N = 65$, $\chi^2_1 = 0.45$, $P = 0.49$; Fig. 3).

<H2>Laboratory results

Overall laboratory background respiration rates contributed in control respirometers were 0.30 μmol/O_2/h. As with the field results, in the laboratory, invulnerable *Nucella* had higher oxygen consumption rates than vulnerable individuals (gamma distributed GLMM: $N = 65$, $\chi^2_1 = 61.48$, $P < 0.001$). However, under laboratory conditions although there was an interaction between treatment and size (gamma distributed GLMM: $N = 65$, $\chi^2_1 = 12.73$, $P < 0.001$), it was vulnerable *Nucella* that showed a reduction in respiration rates by 26.8% under predator risk (Table A1), whereas respiration of invulnerable individuals did not differ between treatments (Table A1, Fig. 4). Once again, differences between size classes were the same irrespective of exposure level (gamma distributed GLMM: $N = 65$, $\chi^2_1 = 1.66$, $P = 0.169$).

<H2>Laboratory behavioural responses

The detection of a predatory cue affected the behaviour of *Nucella*, and its impact was influenced by both prey vulnerability and wave exposure level (Fig. 5). Overall, vulnerable *Nucella* reduced their movement in the presence of a predatory cue, whereas invulnerable *Nucella* did not (negative binomial GLMM: $N = 65$, $\chi^2_1 = 11.84$, $P < 0.001$). Post hoc testing revealed that both size classes moved similar distances in filtered sea water (Fig. 5) but in crab effluent vulnerable *Nucella* reduced their movement (Table A1), whereas invulnerable individuals did not (Table A1). Under predation risk conditions, there was an overall effect of wave exposure on *Nucella* behaviour (Fig. 6; negative binomial GLMM*:* $N = 65$, $\chi^2_1 = 4.92$, $P = 0.03$). *Nucella* from sheltered shores, naturally exposed to higher ambient levels of predation

risk, reduced their movement when exposed to crab effluent (Table A1), whereas *Nucella* from wave-exposed shores remained active (Table A1).

<H1>Discussion

Short-term metabolic responses of invertebrate prey to predation risk and the resulting antipredator behaviour are not well understood (Canero & Hermitte, 2014; Mitchell, Bairos-Novak, & Ferrari, 2017), and the influence of individual vulnerability even less so (DeWitt et al., 1999). Exposing *Nucella* to a predatory cue affected their routine metabolic rate as well as their antipredator behaviour, but each response was influenced differently by individual vulnerability and wave exposure. When vulnerable and invulnerable *Nucella* were exposed to a predatory cue in the field, moments after being collected, it was the invulnerable size class that reduced its oxygen consumption rate, as opposed to vulnerable ones. Note that *Nucella* were not tethered while in the respiration chamber as our intention was to capture the total oxygen consumption related to the detection and subsequent short-term response to predation risk. Therefore, our results do not allow us to distinguish between a potential physiological response to predation risk and the metabolic cost of the resulting behavioural response. Changes in oxygen consumption rates are therefore a combination of stress-induced changes in metabolic rate as well as behavioural changes. Notwithstanding, our results clearly indicate that predation risk may still influence prey that are otherwise safe from direct predation by specific predators. In addition, by comparing oxygen consumption in the field, in individuals extracted directly from natural conditions, with that of individuals maintained in the laboratory, we have also shown important differences in response. Our results and particularly the differences between the field and laboratory observations are explained in relation to size-related risk taking as well as through potential changes in *Nucella* physiological and energetic state.

<H2>Oxygen consumption in vulnerable *Nucella*

When vulnerable *Nucella* were exposed to a predatory cue in the field, there was no change in oxygen consumption when compared to respiration in filtered sea water alone. Previous laboratory-based studies show a cessation of movement in the presence of a predatory cue (Large & Smee, 2010; Vadas et al., 1994). However, our field-based results, when framed from the perspective of foraging–risk trade-off, may be explained by Clark's asset protection principle (APP, Clark, 1994). The APP asserts that foraging decisions relate to the relative amount an individual stands to lose or gain from foraging at a specific time. The APP argues that for a given amount of energy to be gained from foraging at a specific time, smaller individuals have less to lose (less already invested in growth) and proportionally more to gain than a larger individual. In this context, smaller individuals should forage under risky conditions if the potential energy gain is high enough. In essence, it is more favourable for smaller prey to forage during risky periods than larger individuals. Thus, vulnerable *Nucella* under predation risk conditions are likely to continue to search for food due to the high fitness gains, resulting in similar levels of oxygen consumption between our two treatments.

In the laboratory, where *Nucella* were fed *ad libitum* and did not experience risk cues or wave action for one month, oxygen consumption responses to risk differed to those in the field. Vulnerable *Nucella* reduced their routine metabolic rate as well as their movement when exposed to a predatory cue. These seemingly contradictory patterns between field and laboratory results may be explained in the context of the risk allocation hypothesis (RAH). The RAH rests on the inextricable link between current energy reserves and decision making under risky conditions, meaning that behavioural changes are not a result of momentary trade-offs, but rather as forming part of an overarching foraging strategy (Burrows & Hughes, 1991; Lima & Bednekoff, 1999; Lima & Dill, 1990; Mangel & Clark, 1986). In essence, low energy reserves force prey to forage irrespective of risk, whereas when energy reserves are high, prey

are able to wait out risky periods in order to forage during more favourable ones (Lima & Bednekoff, 1999; Lima & Dill, 1990). One of the important predictions of the RAH is that if prey experience prolonged periods of safety interspersed with short high-risk periods, then prey should stop foraging during the high-risk periods (Lima, 1998). In the laboratory, *Nucella* experienced 'safe' conditions, where they were able to increase energy reserves. Thus, when faced with predatory risk they reduced activity as predicted by the RAH which in turn was reflected in a reduction in oxygen consumption. When Matassa and Trussell (2014) tested the response of starved and satiated *Nucella* in the laboratory they found patterns that corroborate our field–laboratory comparisons. Satiated animals did not forage during risky periods whereas starved individuals were forced to forage even under high-risk conditions.

<H2>Oxygen consumption in invulnerable *Nucella*

Although vulnerable *Nucella* reacted predictably to predation risk in terms of the RAH, the pattern seen in the invulnerable adults was less clear. Under field conditions, invulnerable *Nucella* reduced their oxygen consumption rate in response to a predatory cue. Large invulnerable *Nucella* are much more likely than small vulnerable individuals to have sufficient energy reserves to be able to reduce activity in the presence of increased risk (Feare, 1970). Thus, a reduction in oxygen consumption in the field may be a consequence of a reduction in movement. Although the exact mechanism underpinning this reduction in oxygen consumption is beyond the scope of this investigation (stress response and movement), these observations are important in showing that *Carcinus* is still able to affect *Nucella* even after they have reached a size refuge. This pattern changed after *Nucella* had been housed under 'safe' conditions in the laboratory. When tested again in the laboratory, where we expected a similar pattern to that seen in the field (with satiated individuals reducing their respiration as well as their movement), there was no reduction in oxygen consumption or movement under the predation risk condition. Clearly the complexity of behavioural and physiological changes in

379 laboratory-housed *Nucella* at a size refuge warrants further study, as these size classes have a
380 disproportionate influence on population dynamics.

381 **<H2>Antipredator behaviour**

382 Antipredator behaviour was only assessed in the laboratory, and not in the field. Our
383 observations showed an interesting influence of wave exposure (and hence prior experience of
384 predatory threat) on the propensity for *Nucella* to adopt an antipredator behaviour. Wave-
385 sheltered populations (which naturally experience higher predation risk) showed higher levels
386 of antipredator behaviour (cessation of movement) than their wave-exposed counterparts. At
387 the population level, comparisons of the effects of sympatric and allopatric predators on the
388 behaviour of prey have shown that the influence of local ambient predation pressure informs
389 antipredator behaviours (Aschaffenburg, 2008; Large & Smee, 2013; Rochette, Dill, &
390 Himmelman, 1997; Rochette et al., 1999). In comparisons of antipredator behaviour of the
391 common whelk, *Buccinum undatum*, from populations naturally exposed to different suites of
392 predators, Rochette and Himmelman (1996) found that individuals adopt more appropriate
393 antipredator behaviour to sympatric predators than allopatric ones. In *Nucella* investigations of
394 wave exposure effects on behaviour are conflicting. Large and Smee (2013) found that crabs
395 caused a reduction in *Nucella* movement in both wave-sheltered and wave-exposed
396 populations. By contrast, and in accordance with our own work, Freeman et al. (2014) showed
397 lower levels of antipredator behaviour in more predator-naïve populations from exposed
398 shores.

399 **<H2>Potential ecological importance**

400 The changes in behavioural and physiological traits of prey can have potentially cascading
401 effects on the rest of the biological community. A predator's influence on community dynamics
402 is not limited to their regulation of prey densities (density-mediated indirect interactions,
403 DMIIs), but also through their influence on prey physiological and behavioural traits (trait-

mediated indirect interactions, TMIIs). Investigations into the potential strength of DMIIs compared to TMIIs between *Carcinus* and *Nucella* have shown that direct predation and predation risk exert similar influence on the community dynamics of this rocky shore food chain (Trussell, Ewanchuk, & Matassa, 2006a). Our results indicate that this may in fact be an underestimation of the importance of TMIIs as previous studies have only used small size classes of *Nucella* that have lower foraging rates than individuals at the size refuge used in this study (Dunkin & Hughes, 1984). The persistence of the indirect effects of *Carcinus* on *Nucella* even after a size refuge has been reached will mean that TMIIs persist for longer than DMIIs, increasing their ecological importance. The greater impact larger individuals have on resources, combined with the protracted temporal scale at which prey are influenced by predation risk, may result in a considerable underestimation of the overall impacts predators have on an ecosystem.

<H2>Conclusions

Our results provide insight into the effects of predators on prey of differing vulnerability and the potential for antipredator behaviours to be influenced by local environmental factors (wave exposure and hence presumed influence of predation risk). Importantly, we have shown that the influence of a predator may be more far reaching than originally thought, as they are able to affect oxygen consumption of prey even after they are no longer susceptible to direct predation. Our contrasting results from field and laboratory experiments show clearly that understanding of prey state (e.g. physiological/energetic condition which is likely to change dependent on handling and husbandry) is critical in generating a holistic understanding of predator–prey responses (e.g. Matassa & Trussell, 2014). Finally, although not consistent across all responses, we found an effect of wave exposure on antipredator behaviour (cessation of movement) indicating an effect of prior experience of predation risk. Further studies into the potential for predators to indirectly influence prey that are not at risk of direct predation will

enable us to better appreciate the overall influence predators have on the ecosystem they inhabit.

Author Contributions

S.K. and S.J. conceived the study idea and S.K., I.M. and N.W. designed the experiments. S.K. conducted the experiments. S.K., T.C., L.G. and S.J. contributed to the analysis of the data and S.K., T.C., L.G., I.M., N.W. and S.J. contributed to the writing of the manuscript.

Declaration of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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703 Appendix

704

705

706

707 **Table 1** Wave fetch indices for exposed and sheltered sites using the Burrows et al. (2008)
708 map-based method using 32 angular sectors and mean crab number per trap per site

709

710 Site	Wave exposure	Mean fetch (km)	Mean crab number (SE)
711 Moelfre	Sheltered	11.71	54.66 (10.7)
712 Porth Cwefan	Sheltered	26.62	45.66 (4.48)
713 Bull Bay	Sheltered	15.37	23.33 (3.17)
714 Point Lynas	Exposed	55.10	0.00 (0.00)
715 Cemlyn Bay	Exposed	55.64	1.33 (0.88)
716 Trearddur Bay	Exposed	37.89	1.33 (0.88)

717

718

Table 2 Field and laboratory model selection results for the potential influence of predation risk on wave-exposed and wave-sheltered populations of dogwhelks

	Terms removed	*df*	Field	Laboratory	Movement
3-way factorial		11	700.52	619.47	1478.19
2-way interaction	E*T*S	10	700.52	617.67	1476.61
	T*S	9	706.07	619.47	1486.37
	E*S	9	696.98	629.18	1478.99
	E*T	9	696.98	615.74	**1475.10**
Single 2-way interaction	E*S + T*S	8	704.20	627.26	1485.34
	E*T + T*S	8	705.28	629.54	1488.90
	E*T + E*S	8	**696.58**	**616.86**	1478.19
Fixed terms	E*T + E*S + T*S	7	703.37	627.60	1487.41
	T	6	717.00	643.29	1500.16
	S	6	766.94	688.82	1485.59
	E	6	701.87	627.26	1490.31
Single fixed terms	T + S	5	785.58	704.94	1499.03
	E + S	5	715.65	642.90	1503.99
	E + T	5	765.00	687.03	1488.46
Random factor	Site	10	699.21	617.67	1476.19

E = wave exposure, T = risk treatment, S = size (vulnerability). Models were selected using generalized linear square models and corrected Akaike information criterion (AICc) for all dependent variables. Selected models are highlighted in bold.

Table A1 Post hoc Tukey's HSD test results for significant interactions from GLMMs conducted on data from field and laboratory experiments

Experiment	Model	Factor	Contrast	Levels		Combination	Estimate	Z ratio	*P*
Field O_2 consumption	O_2 con ~ Vulnerability + Risk treatment + Wave exposure + Vulnerability * Risk treatment + (1|Site) + (1 | *Nucella* ID)	Risk treatment	No predator	vs	Predator	Vulnerable	-0.0608	-0.609	0.914
						Invulnerable	-0.4573	-5.290	**<0.001**
Laboratory O_2 consumption	O_2 con ~ Vulnerability + Risk treatment + Wave exposure + Vulnerability * Risk treatment + (1|Site) + (1 | *Nucella* ID)	Risk treatment	No predator	vs	Predator	Vulnerable	-0.3379	-5.883	**<0.001**
						Invulnerable	-0.0555	-1.094	0.644
Laboratory movement analysis	Movement ~ Vulnerability + Risk treatment + Wave exposure + Vulnerability * Risk treatment + Wave exposure * Risk treatment + (1|Site) + (1 | *Nucella* ID)	Risk treatment	No predator	vs	Predator	Vulnerable	-1.6137	-5.052	**<0.001**
						Invulnerable	-0.2426	-0.984	0.715
		Risk treatment	No predator	vs	Predator	Sheltered	-1.3559	-4.401	**<0.001**
						Exposed	-0.5004	-1.982	0.157

'Vulnerable'/'invulnerable' refers to level of vulnerability to predators; 'sheltered'/'exposed' refers to level of wave exposure. Statistically significant models ($P = 0.001$) are in bold.

Figure 1 Map of study sites across the Isle of Anglesey, Wales, U.K.

Figure 2 Mean number (± SE) of *C. maenas* caught per trap for exposed and sheltered shores. *$P < 0.01$ (*t* test).

Figure 3 Field oxygen consumption rates (mean ± SE) of vulnerable and invulnerable dogwhelks from sheltered and exposed shores in filtered sea water (no predator cue) and under predation risk (predator cue). Different letters indicate significantly different results from a post hoc Tukey's HSD.

Figure 4 Laboratory oxygen consumption rates (mean ± SE) of vulnerable and invulnerable dogwhelks from sheltered and exposed shores in filtered sea water (no predator cue) and under predation risk (predator cue). Different letters indicate significantly different results from a post hoc Tukey's HSD.

Figure 5 Movement (mean ± SE) of invulnerable and vulnerable dogwhelks from sheltered and exposed shores in filtered sea water (grey bars) and under predation risk (white bars). Different letters indicate significantly different results from a post hoc Tukey's HSD.

Figure 6 Combined movement (mean ± SE) of all size classes of dogwhelks from sheltered and exposed shores in filtered sea water (grey bars) and under predation risk (white bars).

Different letters indicate significantly different results from a post hoc Tukey's HSD.

773 **Figure 1**

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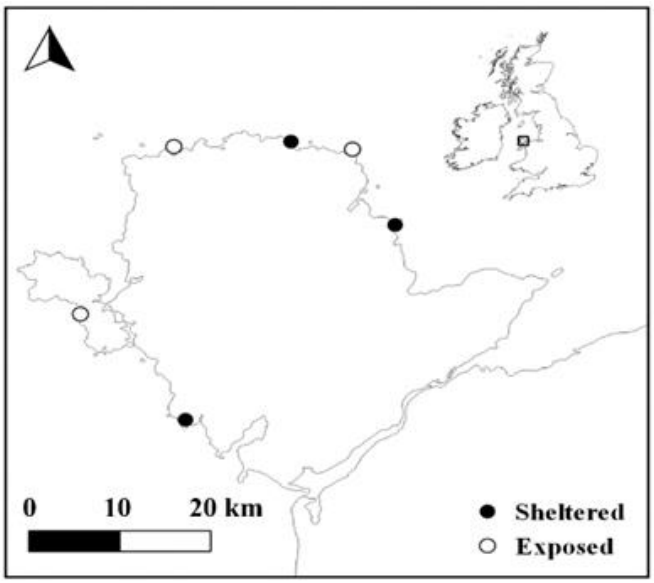

775 **Figure 2**

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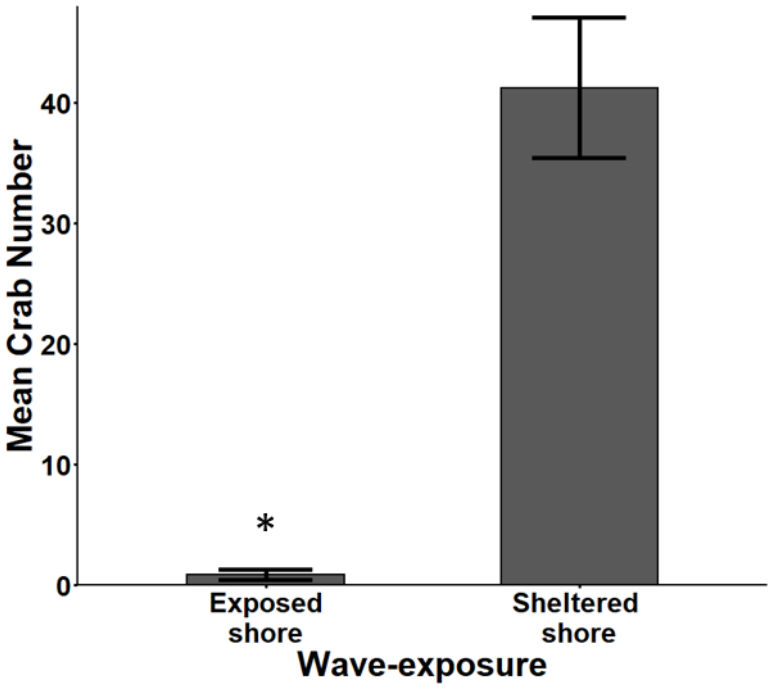

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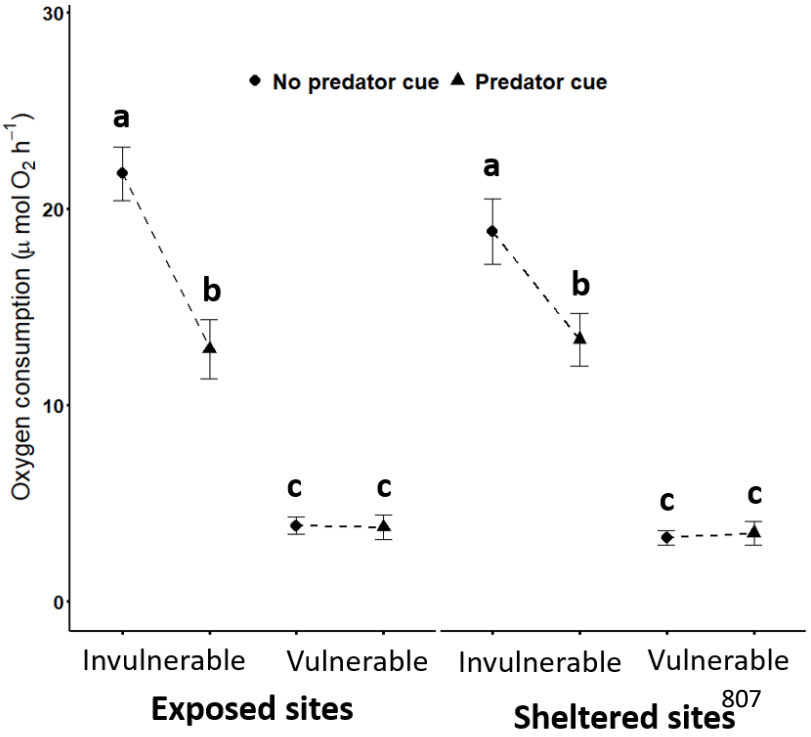
794 **Figure 3**



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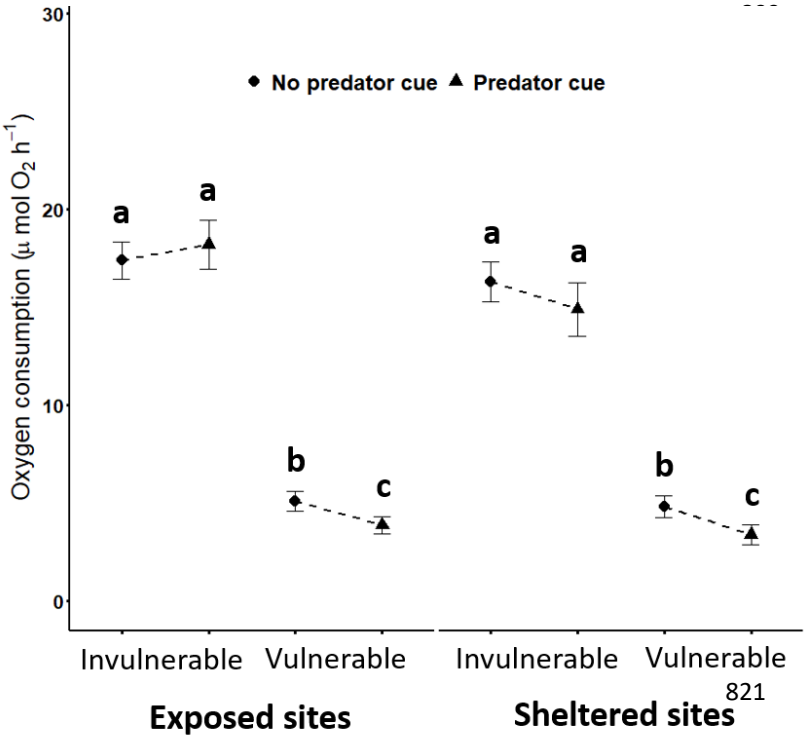
808 **Figure 4**



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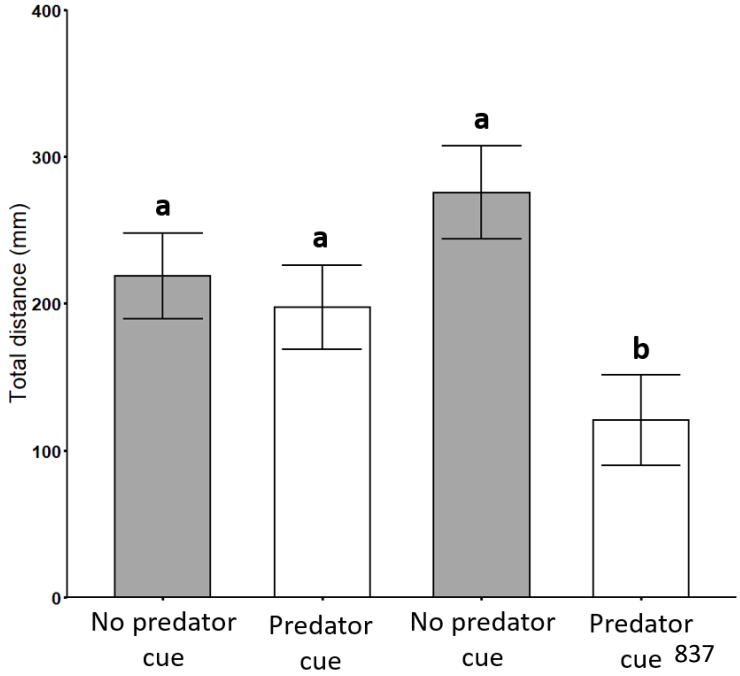
824 **Figure 5**



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838 **Figure 6**